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THE INFLUENCE OF PRECEDING SEASONS ON THE GROWTH OF YELLOW PINE

By J. E. Kirkwood

Many of the mountains of western Montana have no trees on their western and southern slopes, except at altitudes above 4,000 or 5,000 feet. Some support sparse open stands of yellow pine and Douglas fir; in such places the ground cover usually consists of grasses and a few shrubs. The barren aspect of these slopes is due to the desiccating influence of wind and sun, to the full force of which they are exposed throughout the growing season. The annual precipitation in the vicinity of Missoula is 15.84 inches, which represents the mean of over twenty years of observation. May and June are the months of heaviest rainfall, furnishing 4.43 inches of the above mean. By the same reckoning July and August together furnish 1.95 inches of the annual precipitation, and during these months the soil becomes dry to a depth so great that only deeply rooted perennials are able to survive, and these with growth suspended, or at least very much retarded.

Situations on such slopes, locally more favorable, are occupied by incipient forest growth which increases toward the greater altitudes, where, owing to the storage of snow and to other factors, conditions are more favorable for the growth of trees. In this region the yellow pine and Douglas fir are the species most resistent to drouth, encroaching gradually upon the prairie, and eventually occupying it fully or giving way to other species of forest trees. In the margin of the yellow pine type, where the prairie and the forest blend, the conditions for forest growth are

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most severe from the standpoint of moisture requirements as compared with other forested areas. Under such circumstances, therefore, we should expect to see most clearly expressed the

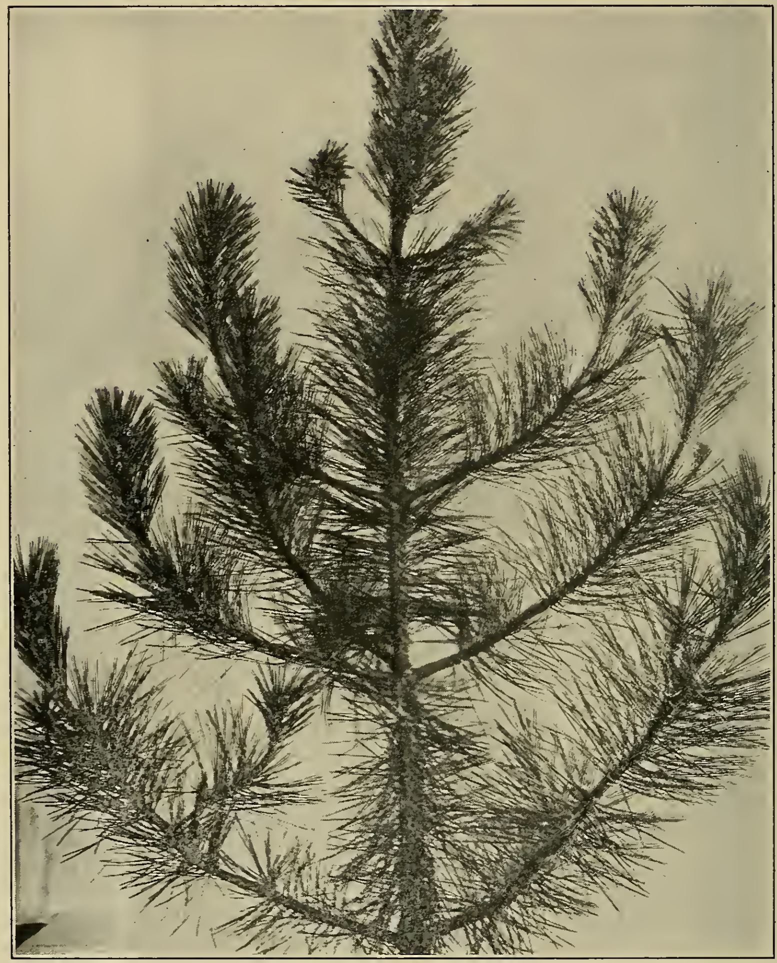

FIG. 1. Part of the crown of a young pine (*Pinus ponderosa*), showing the height growths of the years 1910 to 1913 inclusive.

influence of any variation in the moisture supply from time to time, and especially from year to year.

The relation of the water supply to metabolism and assimilative activity is well known. It is equally well known that the rate of height and diameter increase is the expression of the relative abundance of soil moisture, as well as of other elements in the essential conditions of growth and development. It has been shown that there is a close relation between the annual precipitation and diameter growth in the western yellow pine. Douglas,* working on *Pinus ponderosa* near Flagstaff, Arizona, found that for a period of years the relative diameter of each season, as revealed by careful stem analyses, corresponded closely with the relative abundance of moisture in the several years, as shown by the weather records of that locality. The results of this investigation further showed that the variability in increment was in this instance subject to several factors, such as the relative porosity of the subsoil, the unequal distribution of soil moisture in different directions from the tree, etc.; in short, that any differential distribution of moisture, either topographically or from season to season was expressed in a corresponding variation in the size and form of the annual rings. The conclusions in this paper seem to be supported by the facts presented, and will doubtless apply to other regions as well, where the amount of soil moisture varies considerably from year to year during the period of more rapid growth. Relative height and diameter increase, however, are not always the expression of the conditions in the same season in which such increase took place, but sometimes indicate the factors prevailing in the preceding year. Bogue,† as a conclusion from observations at Stillwater, Okla., states that "the month of maximum rainfall is the month of maximum growth." As a result of further studies at Lansing, Mich., he finds that the width of the ring is proportionate to the rainfall within certain limits, but that excessively heavy or light precipitation is evidenced by a corresponding growth of the tree in the following year, and rightly attributes the difference to the difference in the amount of food material stored in the preceding season.

* Douglass, A. E. Weather cycles in the growth of big trees. Monthly Weather Review **37**: 225–237, June, 1909.

† Bogue, E. E. Annual rings of tree growth. Monthly Weather Review **33**: 250–251, June, 1905.

The main growth of trees in height and diameter is accomplished during the first few weeks of the growing season. The opening of the buds in the spring or early summer is followed by the rapid elongation of the shoot of the season, and the early expansion of its leaves. There after-growth in length is very much retarded, and finally ceases with the formation of the terminal bud, which is to be unfolded in the following season. This terminal bud is formed long before the summer is over and into it are crowded the nutritive substances which supply the food for its early expansion the following year. Upon the size and vigor of the buds thus formed depends the length of the shoot of the following season, other things being equal. Likewise the size and vitality of the bud are measures, in the main, of the conditions obtaining in the seasons in which they were formed. The greater the supply of moisture, up to the optimum degree, the more favorable the temperature, sunlight, etc., the greater is the reserve force in the buds and consequently the more vigorous are the shoots issuing from them.

It is improbable that the whole growth of the new leader is at the expense of the food stored in the bud alone. That from other parts also doubtless contributes, but the tendency is to crowd the formative materials toward the extremities of the main shoot and the branch. In the sharing of these materials the main shoot leads and the branches follow in the order of their importance. The principal growth, however is undoubtedly at the expense of the locally stored materials, the substances stored elsewhere having their part to play in the development of the tissues in their immediate proximity.

An examination of the buds reveals the cells of the leaf rudiments and axis densely crowded with a granular material which appears to be proteid, responding to several tests for that substance. This is in line with what is known concerning the nature of reserve materials in trees. The density of the stored substance is greatest in the bud, and much less in the stem outside of the bud.

It is a matter of no difficulty to determine by external markings the limits of annual growth on the younger portions of the stem and branches of most woody plants. Sometimes it is possible to trace the annual growth back through twenty five or thirty years by reference to the branching system. *Pinus ponderosa* is a favorable subject for study in this particular. At the top of the leader a strong bud is formed toward the conclusion of the growing season. Close to the base of this bud are formed several lateral ones, the subsequent development of which produces a whorl of branches. As other lateral buds are usually lacking along the shoot of the season, it follows that each circle of branches marks the limit of a season's upward growth of the main stem. As the internodes, or spaces between successive circles of branches, do not increase in length after they are first formed, the height increment of all the past seasons can be determined, so far as one is able to identify the distinct whorls which mark the conclusion of each year's growth.

That the length of the internode in the western yellow pine growing in dry situations is an expression of conditions affecting growth, not in the present, so much as in the preceding season, is now shown with remarkable clearness by the trees of this region.* Some of the facts here set forth were observed on an island in Flathead Lake during the summer of 1913. Trees were growing at altitudes varying from four or five to one hundred feet above the level of the lake, and in the more open places among the mature trees many younger individuals were present varying from four to fifteen feet in height. Of many of these it was observed that the internode for 1911 was considerably shorter than that for 1910. Reflecting upon the fact that the season of 1910 throughout the whole region was exceptionally dry, and that of 1911 much more favorable, the question arose as to the apparently contradictory evidence of the internodes. Why should the growth be less in a season supposedly more favorable, and greater in a season obviously less advantageous?

It is evident that the growth in length in each season is not directly affected in this region by the lack of rain in July and August, since the elongation of the shoot is practically ended before the dry season sets in and before the moisture from winter

* Pfeffer, W. Plant Physiology, Vol. I, p. 603.

snows and spring rains disappears from the soil, but indirectly by the drouth in the months indicated, as affecting the supply of reserve food in the buds and other parts. The supply of food stands in direct ratio to the condition of several factors, among which the amount of available moisture is very influential, during the middle and later summer of the season next preceding. As a lack of moisture affects adversely assimilative and other activities, a meager store of nutritive materials would be the result of a dry summer, and would find expression the following year in reduced growth in length of all the new shoots. Of course this weakness of the buds would not occur in trees as a result of diminished precipitation in situations providing adequate soil moisture throughout the season, but only where drouth appears early, as is usually the case on southern and western slopes. For this reason those trees in the locality mentioned which grew nearer the water level showed no such inequality in the length of the internodes, and the same was found to be true in more favored situations elsewhere.

It is true, of course that assimilation can take place at all seasons in evergreens, under proper conditions of temperature and illumination. It has been shown that assimilation may proceed in some plants at a temperature as low as $-40°$ C., and that in pines and spruces the process is active at $3°$ to $5°$ C. In the northern Rocky Mountain region, however, the temperatures are considerably below $0°$ C. during most of the winter, and frequently below $-40°$ C. The soil, moreover, is frozen to a depth of several feet, resulting in a reduction of the water supply. In this problem, however, it is chiefly a question of relative activity and not of complete suspension of photosynthesis at any time, while we are dealing with reserve material in the form of proteid, not starch, nevertheless the synthetic activity of the tree, so far as this material is concerned, is closely associated with starch formation, according to the best evidence at present available.

Seeking further evidence on the relation of the growth of yellow pine to the distribution of rainfall, the writer made two series of observations in the vicinity of Missoula, the results of which are given in the accompanying tables. Where the forest borders on the grass land strips of timber afforded convenient material for study. In these cases the stand was a mixture of yellow pine and Douglas fir, varying in height from five to twenty-five or thirty feet. One of these areas occupies one slope of a shallow, narrow valley which traverses in a direction from southeast to northwest, the barren western slope of Mt. Sentinel, southeast of the town of Missoula. The timbered slope of the valley faces the northeast, its opposite slope facing southwest is treeless. Along the edge of this stand, a strip over a quarter of a mile in length and about fifty yards in width provided the 42 young yellow pines whose measurements are here recorded. All the pines up to thirty feet in height were measured, except such as showed evidence of injury in the parts concerned.

In Table I the height growth is shown of each of the five seasons, 1909 to 1913 inclusive. The measurements are in inches. It will be observed that practically every one of the pines growing on this area exhibited a growth during the season of 1911 considerably less than that of either of the two seasons preceding or following, and that, although the difference in a few cases is reduced to zero, in nearly all of the individual cases the difference between the growth of 1911 and that of the other seasons amounted to several inches. The same relation appears conspicuously in the totals and again in the averages, but the most significant fact seems to be in the absence of exceptions to the general rule.

Table II presents the results of similar measurements on another area near Missoula about two miles from the first. Only a few observations were recorded in this case, as practically every tree approached showed the same condition.

If one compares these measurements with the weather data given in Table III he will find that the lengths of the internodes stand in relation to the conditions of the seasons in the manner suggested above. The mean precipitation and temperature

* Miyake, K. On the starch of evergreen leaves, and its relation to photosynthesis during the winter. Bot. Gaz. 33: 321–340, 1902.

† Jumelle, Rev. Gen. de Bot. 4: 263, 1892. Pfeffer's Physiology of Plants, Vol. I, p. 338.

‡ Green, J. R. Vegetable Physiology, p. 174. 1911.

Table I

Approximate Measurements of the Height Growth of *Pinus ponderosa*, Made on the Upper Portions of the Main Stem, for Each of the Seasons Indicated, in Inches

No.	1909	1910	1911	1912	1913
1	8	8	5	6	8
2	6	8	4	5	6
3	5	5	4	4	6
4	10	10	6	10	10
5	6	9	3	6	8
6	8	8	5	6	9
7	9	8	8	3	8
8	8	6	6	5	5
9	8	6	5	9	9
10	13	12	8	11	13
11	12	9	8	12	14
12	7	7	5	7	11
13	8	8	7	11	12
14	12	13	11	14	13
15	12	12	6	10	12
16	4	10	6	11	14
17	11	12	8	12	12
18	9	10	7	11	12
19	11	11	7	11	12
20	12	11	6	8	12
21	10	12	6	10	10
22	12	12	6	7	9
23	14	14	10	15	14
24	14	14	11	10	12
25	14	20	6	16	14
26	14	10	12	14	14
27	14	10	10	14	13
28	13	11	5	12	13
29	14	15	10	13	14
30	12	13	10	11	12
31	10	14	11	13	14
32	11	14	11	14	14
33	13	8	6	12	12
34	8	8	9	11	8
35	10	13	12	13	14
36	12	13	12	12	12
37	10	11	4	12	14
38	12	13	9	13	12
39	13	13	11	14	15
40	8	13	9	12	16
41	12	15	7	13	16
42	8	8	6	10	12
Total.......	437	457	318	443	490
Average.....	10.4	10.88	7.57	10.54	11.66

records are given for the months April to September inclusive for the years represented by the measurements. The temperature is important in this connection as affecting the rate of transpiration of the trees and the rate of evaporation from the soil. The season of 1909 was marked by ample rainfall in June and July, and by temperatures, during the earlier part of the season, lower

Table II

Measurements on the Same Basis as Shown in Table I, but of Trees on a Different Area

No.	1909	1910	1911	1912	1913
1	10	10	9	11	—
2	8	10	7	9	12
3	10	6	4	5	7
4	7	8	6	9	9
5	6	7	6	8	11
6	7	8	7	11	10
7	7	7	4	8	8
8	7	7	5	8	8
Total.......	62	63	48	69	65
Average.....	7.75	7.75	6	8.37	9.28

than those of any of the other years here recorded. Precipitation was least in 1910, and of the rain of this season over 40 per cent. fell in September, too late to be of much influence in the formative work of the year. The months of June and July were marked by only four fifths of an inch of rain, and by temperature higher than usual, which served to intensify the drouth during

Table III

Weather Data for Missoula, 1909 to 1913 Inclusive, April to September
T. = temperature, F.

Mo.	1909		1910		1911		1912		1913	
	Rain	T.	Rain	T.	Rain	T.	Rain	T.	Rain	T.
Apr....	1.19	40	0.66	51	0.72	43	2.02	46	1.46	45
May...	0.99	50	1.92	56	1.00	51	3.09	52	1.44	52
June...	2.65	60	0.67	63	3.38	62	1.78	62	2.39	62
July...	3.52	65	0.13	71	0.21	66	1.94	63	1.52	67
Aug....	0.34	66	0.57	62	0.43	64	1.88	63	1.52	67
Sept. ..	2.38	57	2.76	56	1.31	54	1.58	50	0.74	57
Total ..	11.07		6.71		7.05		12.29		8.58	

the very period in which most of the new tissues were taking form. This period was followed by another month of dry weather, in which the slight amount of rain which fell could have had no appreciable influence, and during which the synthetic activity of the tree must have been greatly retarded. The year 1911 was marked by a more advantageous distribution of the rain, 3.59 inches falling in June and July, as compared with .8 of an inch in the same part of the previous year, and this season's advantages were clearly expressed in the ample growth of the shoots in the following season. Likewise the season of 1912 was an exceedingly favorable one for forest vegetation in this region, as testified by the excellent growth of all shoots in 1913.

A series of observations of a similar nature was conducted also on the Douglas fir, growing with the yellow pine in the same area which furnished the data given in Table I. Twenty-three trees were measured, these trees being of about the same age as the pines. From the figures given it will be apparent that the com-

Table IV

Approximate Measurements of the Height Growth of Douglas Fir (*Pseudotsuga taxifolia*), made on the Upper Portions of the Main Stem, for Each of the Seasons Indicated, in Inches

No.	1909	1910	1911	1912	1913
1	12	13	8	14	12
2	6	9	6	11	11
3	13	11	10	13	12
4	13	12	13	12	10
5	11	10	12	12	12
6	13	13	10	14	14
7	14	12	8	14	14
8	11	12	11	14	12
9	8	14	13	12	8
10	8	11	8	13	12
11	13	13	13	14	13
12	13	12	12	14	14
13	10	12	13	14	12
14	12	10	6	14	13
15	16	12	6	14	16
16	12	14	10	12	12
17	15	14	10	14	14
18	9	8	10	12	12
19	5	8	6	10	12
20	12	11	8	10	10
21	12	8	6	13	12
22	14	13	12	15	14
23	10	11	8	8	12
Total.......	262	263	219	293	283
Average.....	11.4	11.4	9.5	12.7	12.3

parative lengths of the internodes are not so uniform as in the case of the pines, there being some instances in which the longer internode falls in the year 1911, instead of the shorter. The reason for these exceptions is not clear; they may possibly be due to local variations in the soil moisture. The totals and the averages, however, show the same relations to one another as in the case of the pines. The figures are given in Table IV.

It is evident of course that the influence of the preceding season is not limited to the retardation of height growth during the year immediately following, but that the shorter twigs must involve the production of a lesser leaf area than usual, which must in turn be reflected in the amount of reserve products accumulated. Here, however, the problem becomes complicated, and the lessened leaf area on the last shoot may in a measure be compensated by the greater illumination of the older leaves, by this fact made possible. The figures for 1912 as compared with those for 1913 in Table I would seem to indicate the holding over effect as here suggested, though the same does not appear to be true of the Douglas fir. It is also evident that trees of different species on the same areas are not equally responsive to the variations of soil moisture in the manner indicated, a fact which probably is due chiefly to a difference in the degree of tolerance though to some extent to other specific peculiarities.

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A NEW SOUTHWESTERN SEDGE

By Kenneth K. MacKenzie

Since writing the article on *Carex* for the Illustrated Flora two species have been found by Mr. E. J. Palmer in southwestern Missouri not included therein. One is *Carex arkansana* Bailey, heretofore known from Arkansas and Oklahoma. The other is an undescribed species bearing a remarkable outward resemblance to the European *Carex vulpina* L., and in technical characters intermediate between that species and our own *Carex stipata* Muhl. It is represented in the collections at the New York Botanical Garden by several specimens, and seems first to have